ADMINISTRATIVE STUDY OF RELATIONSHIPS BETWEEN WILDLIFE AND OLD-GROWTH FOREST STANDS, PHASE III

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A report of work performed for the Pacific Southwest Region

USDA Forest Service

Supplement RO-44 under Master Agreement No. 21-395

Written by Martin G. Raphael, Kenneth V. Rosenberg and Cathy A. Taylor

September 30, 1982

Thesis/
Reports
Raphael,
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INTRODUCTION

The management of old-growth Douglas-fir (Pseudotsuga menziesii) forests has become a controversial issue in the Pacific northwest, primarily because of the possible value of old-growth as habitat for certain wildlife species versus the revenues represented by old-growth trees (Meslow et al. 1981, Harris et al. in press). Management of old-growth forests to provide wildlife habitat requires detailed knowledge of their ecology including an inventory of associated wildlife species, an assessment of the old-growth dependency of those species, and an analysis of the size and distribution of habitat patches necessary to support viable populations of those species (Burgess and Sharp 1981).

This study was initiated in October, 1979. A cooperative effort of the USFS, Region 5, and U.C. Berkeley, it is designed to:

1. Evaluate methodologies to inventory wildlife in old-growth stands;
2. Conduct an inventory of birds, mammals, reptiles and amphibians present in old-growth stands;
3. Describe relationships between the structural features of old-growth stands and wildlife; and
4. Develop models to predict the consequences of silivicultural treatments in old-growth on wildlife populations.

This report summarizes our progress over the past 12 months. Our first report (Raphael et al. 1980) emphasized objective 1; the second (Raphael et al. 1981) addressed objectives 2 and 3. This report also emphasizes these 2 objectives in light of a second full year of data collection. We focus on comparisons of wildlife abundance and diversity along a gradient of stand ages ranging from sawtimber to old-growth. We do not address stand

size relationships in this report. A preliminary evaluation of such effects is presented by Raphael (in press).

ACKNOWLEDGMENTS

We thank John Brack, Cathy Brown, Chris Canaday, and Larry Jones for field assistance and data analysis. Lori Merkle, Andra Strads, Wendy Waggoner, and Mickey Whiteford helped administer the project. We also thank the personnel of the Lower Trinity, Big Bar, and Ukonom River Ranger Districts for their cooperation. We especially thank Bob Nelson and Hal Salwasser, USFS, as well as the staff of Region 5 for their continuing support of this project. We also thank Reg Barrett for allowing us the freedom to make a mistake and for trusting us to correct it.

METHODS

Most of our sampling methods are described in earlier reports (Raphael et al. 1980, 1981). To summarize, we selected 136 study plots within 46 stands distributed among the Six Rivers, Klamath, and Shasta-Trinity National Forests in northwestern California. At each plot center (marked by flagging) we census birds and diurnal squirrels using a variable radius plot, we estimate abundance of small mammals, reptiles and amphibians using a 2 x 5 array of pitfall traps, we determine presence of larger mammals using a baited, smoked-aluminum track station, and we measure characteristics of vegetation and downed wood on 3, 0.04-ha, circular plots located at random distances from the plot center.

On a subset of plots, we estimate abundance of small mammals using grids of Sherman livetraps typically arranged in a 10 x 10 array Additions and changes to procedures described in our earlier reports are detailed below.

Stand Age Determination

A primary objective of our study is the comparison of wildlife communities in relation to stand successional stage. When stands were originally selected, we used USFS timber stratum labels for stratification. These labels are derived from aerial photography based on average crown diameter of the overstory trees. We selected equal numbers of stands in each of 3 habitat classes (D3 = 13-24 feet, D4 = 25-40 feet, D5 = >40 feet).

We encountered several difficulties using these strata. First, Shasta-Trinity does not recognize the D5 stratum; rather, they lump all potential D5 stands under the D4 label. Secondly, it was apparent to us that within-stand heterogeneity was so great that different plots within one stand could actually be classed in a stratum different from the one assigned to the stand as a whole. Primarily for these 2 reasons, we decided to use our on-the-ground vegetation data to restratify the plots.

Our approach was to calculate an index of stand age based on the stem diameter distribution of trees included in the 3 circular plots sampled at each site. This index of stand age was calculated using a weighted average of the estimated ages of all softwood trees counted in the 3 subplots. The average was weighted by multiplying the estimated age of each tree by its basal area, summing the product over all trees, and dividing the sum by total basal area. In this way, small trees, which were numerous, had less influence on stand age than if each tree was counted equally regardless of diameter. Because of constraints on time and money, it was not possible to bore each tree to estimate its age. Rather, we estimated ages by placing each tree into one of 7 diameter at breast-height (DBH)

classes and then assigning to all trees within a particular class the average age of trees in that class (derived from extensive data on file at Lower Trinity Ranger District). Tree DBH may be poorly correlated with age because of differences in site quality and stocking density. Nonetheless, we feel that, in general, larger-diameter trees are older and that this age estimate is sufficient as a relative index to a stand's successional stage. All references to stand age elsewhere in the text refer to this age index.

To stratify plots for comparisons, we used 3 age-index classes. Age class 1 (AC1) includes all plots that had stand ages <150 years, age class 2 (AC2) included plots 150 to 250 years, and age class 3 (AC3) included all plots >250 years old.

Bird Census

Birds were censused in the manner described earlier (Raphael et al. 1981). We sampled winter birds from 8 January through 19 March, 1982. We encountered severe problems with poor access to plots due to snow and with long periods of precipitation which prevented censusing. Therefore, the census started later and took longer this year compared with winter, 1981. Spring censuses began on 4 May and ended on 15 June, 1982. Censusing logistics were similar to 1981.

To calculate an estimate of total density of all bird species in each plot, we analyzed the pooled sample of bird observations for a plot using the FOURIER estimator of program TRANSECT (Burnham et al. 1980). We found that this is a more accurate method than summing the density estimates of individual species over a plot. In addition, last year we calculated spring densities of each bird from the maximum count of that bird on any of the 4

visits. This year, we calculated the average count over all 4 visits. Thus, our density estimates are lower than those reported last year. Consequently, we reanalyzed data from last year to ensure comparable values. It is also important to note that we have made no attempt to double-count singing males (to account for non-singing females). Density estimates for individual species were used to test for associations with stand age and to corroborate year to year changes, but are not presented in this report. Percent frequencies of occurrence of each species in each season are presented at this time as a relative index of abundance.

Owl Census

We began our nighttime owl survey earlier this year compared with last. Censusing began 23 March and ended 24 May this year versus 13 May to 2 July last year. We consciously sampled earlier this year in an attempt to match peak calling times of Saw-whet, Spotted, and Flammulated Owls. We were careful this year to sample each plot both before and after midnight.

Pitfall Traps

We changed our pitfall procedures this year. Rather than rely on a single, short trapping period where bear damage can exert significant effects, we now run the pitfalls continuously without bait or water. We checked them on each entry to a point during the course of bird censusing (4 visits in winter and 4 in spring) or other work; usually at 3-week intervals. We avoided baiting traps to reduce bear damage and did not fill with water for practical reasons. It is nearly impossible to maintain adequate water levels by backpacking water over the terrain typical of our study sites. However, in winter many of the traps contained some water

which entered naturally.

In addition, we replaced one 2-gallon bucket with a 5-gallon bucket at each point in an effort to sample mice (deeper buckets prevent escape). Also, we replaced half of the 30 x 30-cm plywood covers with larger (41 x 81 cm) covers to provide a more attractive artificial shelter for reptiles and amphibians.

To estimate relative abundance of species captured in pitfalls, we counted all captures recorded in 3 trapping periods (winter, spring, summer) and divided the captures by the number of trapnights (calculated by deducting all buckets destroyed by bears and summing the remaining buckets over the days between trap checks). Because of the long intervals between capture periods, we did not attempt to calculate population estimates using removal estimators. Such an estimate would surely be invalid because the crucial assumption of population closure during the sampling period was unlikely.

Because of difficulty in separating 2 shrew species (Sorex trowbridgii and Sorex vagrans) in the field, both are considered as Sorex (spp.) in this report. Voucher specimens await identification by taxonomic experts.

Track Stations

Track stations were monitored in 3 successive periods from 9 August until 15 September. Methods were identical to those reported earlier (Raphael et al. 1981) except that we were careful this year to preserve tape impressions of all tracks for purposes of developing a standardized description of each species' tracks.

Livetrap Grids

Due to the preponderance of livetrap grids in AC2 plots, an additional 3 grids were established in 1982, 1 in AC1 and 2 in AC3. All new grids were

arranged in 10 rows of 10 traps each spaced at 20-m intervals. We ran the traps in 3, 6-day sessions between 5 July and 24 July 1982, using the same methods reported by Raphael et al. (1981). In addition, however, we recorded precent ground cover (rock, bare ground, litter, herbaceous cover) shrub cover (% cover of all plots <2.0-m tall) and tree cover (% cover of all plots >2.0 m tall) on a 25-m^2 quadrat around each trap. These data are being analyzed and will be included in a later report.

Population estimates were calculated for each plot by pooling captures of all species using the computer program CAPTURE (March 1982 version, Otis et al. 1978, White et al. 1982). Density estimates proved unrealistic using this program. Instead of using the computer-generated estimates, we first calculated grid area by adding a boundary strip to each grid determined from the average inter-trap distance measured over all captures of all animals, then divided the CAPTURE-derived population estimate by this computed grid area.

We also encountered 2 taxonomic difficulties. First, the Townsend Chipmunk has recently been split into 4 species (Sutton and Nadler 1974). We believe that all of our Tamias are Allen's chipmunk (T. senex) but are awaiting results of laboratory analysis of voucher specimens to confirm this. We may possibly encounter the Sonoma Chipmunk (E. sonomae) on plots adjacent to open areas. Again, laboratory analysis will confirm this. Secondly, we are probably encountering 2 shrew species, Sorex trowbridgii and S. vagrans. For this report, both are pooled as Sorex spp., as in the pitfalls results.

Intensive Herpetofauna Search

Some reptiles and amphibians are unlikely to fall into pitfalls or,

because of their climbing ability, are able to escape. We were especially concerned that our pitfall captures did not adequately reflect salamander abundance. Therefore, we conducted a more intensive search over a subset of plots after the fall rains in November, 1981. A 2-person team searched under all movable objects and broke apart softer logs on each of the 3 vegetation subplots on 27 plots (total area surveyed equals 0.12 ha per plot). In addition, a 20-m^2 quadrat within each of the 3 subplots was searched by systematically raking through all surface litter and duff to the mineral soil. All loose rocks exposed by raking were also turned. Each captured animal was identified, sexed, measured, and released. Other data recorded included a description of the species, size, and decay class of the substrate where an animal was found, its vertical position (on ground surface, under litter, under duff, etc.), horizontal position (on stream bank, near pond, away from stream or pond, etc.), and the depth of the duff layer where the animal was captured.

Avian Foraging Behavior

Beginning in January 1982, observations of foraging birds were made in conjunction with avian censusing. The goals of this preliminary effort were to 1) confirm foraging guild classifications for bird species in Douglas-fir forests, 2) determine precise resource requirements of birds on the study plots, and 3) assess the feasibility of collecting foraging data in conjunction with other phases of fieldwork.

Whenever a foraging bird was encountered, an attempt to collect the following data was made: bird species, sex, age, foraging technique (glean, hover, hawk, peck, etc.), bird height above ground, specific location and substrate to which bird's activity was directed, perch diameter, proximity

to trunk, tree species, tree height and tree DBH. Time of day, sample plot, and appropriate weather data were also recorded. A maximum of five observations of an individual bird were taken at any one time.

RESULTS

Plant Characteristics

Our reclassification of plots based on a calculated stand age index resulted in shifts involving about half of the plots (Table 1). The D3 plots were split equally among AC1 and AC2. The D4 plots were split between AC2 and AC3 as were the D5 plots. The new classification resulted in sample sizes of 35, 62, and 39 plots in AC1, AC2, and AC3, respectively (Table 1). Mean age indices in the 3 classes are 119, 205, and 277 years; these ages correspond to sawtimber, mature, and old-growth classification used by others in the Pacific Northwest (Franklin et al. 1981, Harris et al., in press).

Tree and dead wood characteristics are compared among age classes in Table 2. Basal area of Douglas-fir, tanoak (Lithocarpus densiflorus) and other oaks (Quercus spp) differ significantly in each age class. Basal area of Pacific madrone (Arbutus menziesii), big-leaf maple (Acer macrophyllum), and standing dead trees differed between AC3 and AC1. Duff depth and downed wood volume (≥ 8 cm diameter) also differed between the oldest and youngest age classes. Considering all of these vegetation characteristics, it is apparent that the 3 age classes are distinct from each other, and that the oldest and youngest stands show the greatest dissimilarity (see also Table 4).

Bird Populations

A total of 94 species were detected during 4 seasons of avian censusing (Table 3). Three species were censused only in winter, and 39 only in spring.

Table 1. Relationship of timber stratum classification of study plots to age classes of same plots derived from sampled tree diameters.

New Classification (Age class, years)	Old Classification (Stratum) D3	D4	D5	Totals
< 150	24	6	5	35
150-250	23	22	17	62
> 250	1	23	15	39
Totals	48	51	37	136

Table 2. Comparison of selected vegetation characteristics among stand age-classes.

Category	Age Class Index[1]		
	< 150	150-250	> 250
Basal Area (m^2/ha)			
All trees	46.1^{a}	60.1^{b}	73.6^{c}
Douglas-fir	22.2^{a}	37.9^{b}	49.2^{c}
Pacific madrone	7.6^{a}	3.7^{b}	4.1^{b}
Big-leaf maple	0.5^{a}	0.5^{a}	1.6^{b}
Tanoak	1.9^{a}	8.0^{b}	15.0^{c}
Other oaks (Quercus spp)	10.1^{a}	4.5^{b}	1.3^{c}
Dead trees	3.9^{a}	$5.5^{a,b}$	7.0^{b}
Litter depth (cm)	$6.2^{a,b}$	5.2^{b}	7.3^{a}
Duff depth (cm)	2.7^{a}	3.9^{b}	4.1^{b}
Downed wood volume, < 8 cm^2	11.8^{a}	12.2^{a}	12.4^{a}
Downed wood volume, > 8 cm^2	34.2^{a}	47.3^{a}	71.0^{b}

[1]Superscripts indicate significant differences in Duncan's multiple-range tests. Values with same letter are not different ($p < 0.05$). Sample sizes < 150 = 35, 150-250 = 62, > 250 = 39.

[2]Metric tons per ha.

Table 3. Bird species recorded in Douglas-fir forests in winter and spring, 1981 and 1982. Sample sizes are: <150 years (n = 35 plots), 150-250 years (n = 62 plots), and > 250 years (n = 39 plots).

Species[a]	Percent Frequency among Age Classes												Association with Stand Age[b]							
	Winter						Spring						ANOVA Test[c]				Correlation[d]			
	< 150		150-250		> 250		< 150		150-250		> 250		Winter		Spring		Winter		Spring	
	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82
Turkey Vulture[e]							15	9	4	6										
Goshawk	3	3	3		3							3								
Sharp-skinned Hawk		6	5	6	3	3	12	3	2	5		3								
Cooper's Hawk					3	3	3	3	2	2		3								
Red-shouldered Hawk[e]								9												
Red-tailed Hawk	6	6	8	5	6	5	9		11	3	8	3								
Golden Eagle[e]			3					3												
Peregrine Falcon[e]							3													
American Kestrel[e]		3		2						2										
Blue Grouse	3		6	5	3		6	11	6	10										
Ruffed Grouse			2	3		3	6	6	3			3								
California Quail[e]							3	3												
Mountain Quail	6	6	7	11	3	5	56	23	50	21	43	18								
Band-tailed Pigeon			8		11		3	6		3		2								
Mourning Dove[e]				2						2										
Western Screech Owl			2				26	6	9	2	10	8							-	
Flammulated Owl									5											
Great-horned Owl							3			2		3								
Northern Pygmy Owl	6	3	3	11	3		15		10	12	20	3								

Table 3. Cont.

Species	Percent Frequency among Age Classes												Association with Stand Age[b]							
	Winter						Spring						ANOVA Test[c]				Correlation[d]			
	< 150		150-250		> 250		< 150		150-250		> 250		Winter		Spring		Winter		Spring	
	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82
Spotted Owl	3	3	2	2			11	12	18	23	18	23								
Northern Saw-whet Owl									6	2	5	5								
Common Nighthawk[e]							1													
Vaux Swift[e]							3	6	2	3										
Anna's Hummingbird	3						3	3		6	3	5								
Other Hummingbirds							6	9	13	16	10	13							+	
Northern Flicker	63	34	43	32	48	18	85	46	86	40	65	36								
Pileated Woodpecker	35	34	26	24	31	31	52	51	37	53	23	51			-		-			
Acorn Woodpecker	32	20	28	27	36	26	27	23	13	29	35	28								
Red-breasted Sapsucker	6	11	5	10	3	13	35	31	43	52	48	44								+
Hairy Woodpecker	46	40	48	37	37	39	68	49	53	53	36	62							-	
Downy Woodpecker	3	6	3	6		5	9	9	2	5	3	3								
White-headed Woodpecker				3				3		2										
Hammond's Flycatcher[f]							26	31	35	40	41	44				+				
Dusky Flycatcher[e]								9		3		5								
Western Flycatcher							94	100	100	100	100	100							+	
Western Wood Pewee							48	31	37	31	35	26								
Olive-sided Flycatcher							21	34	32	37	46	33							+	
Rough-winged Swallow[e]								6												
Tree Swallow[e]	3							3	2											

Table 3. Cont.

Species	Percent Frequency among Age Classes												Association with Stand Age[b]							
	Winter						Spring						ANOVA Test[c]				Correlation[d]			
	< 150		150-250		> 250		< 150		150-250		> 250		Winter		Spring		Winter		Spring	
	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82
Violet-green Swallow[e]				10		5		6		3										
Gray Jay										2		3								
Steller's Jay	89	80	62	55	61	54	94	94	97	98	93	100					-	-		
Scrub Jay[e]			3				3			2										
Common Raven	74	54	53	52	68	44	57	23	38	32	48	38					-			
Chestnut-backed Chickadee	94	83	94	85	93	82	100	86	98	84	100	100			+				+	+
Mountain Chickadee[e]		6								2										
Bushtit	9	14	7	5	18	3	9		18	6	13	2								
White-breasted Nuthatch	6	9	6	6		10	3		5	6		13						+		
Red-breasted Nuthatch	77	37	79	35	73	33	70	91	75	94	55	92								
Brown Creeper	77	94	97	94	83	100	85	80	91	94	63	87	+			-	+		-	-
Wrentit	9	2	5	3	5	12	13		26	5	26	10								
Dipper[e]	3																			
House Wren							6	9	15	10	15	8								
Winter Wren	67	86	65	84	75	85	27	14	24	55	30	56				+				+
Bewick's Wren							3		2		3									
American Robin	52	40	58	11	61	10	68	69	62	71	41	51	+	-	-		+	-	-	-
Varied Thrush	79	74	79	71	85	74											+			
Hermit Thrush	9	37	8	15	3	5	47	46	56	61	93	85			+	+	-	-	+	+
Swainson's Thrush[e]									2	2		3								

Table 3. Cont.

Species	Percent Frequency among Age Classes												Association with Stand Age[b]							
	Winter						Spring						ANOVA Test[c]				Correlation[d]			
	< 150		150-250		> 250		< 150		150-250		> 250		Winter		Spring		Winter		Spring	
	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82
Western Bluebird	3	3	5	2	6	5			2		3									
Townsend's Solitaire	12	14		2	3		38	34	48	50	35	46								
Cedar Waxwing[e]								3												
Golden-crowned Kinglet	85	91	94	94	95	90	61	51	84	69	83	82	-		+	+	-		+	+
Ruby-crowned Kinglet	79	49	76	30	68	23							-	-			-	-		
Starling[e]							6													
Hutton's Vireo	92	51	77	48	76	49	94	66	90	65	81	69			+					
Solitary Vireo							94	94	97	94	93	82			-	-			-	-
Warbling Vireo							49	57	50	56	71	74			+	+			+	+
Orange-crowned Warbler							18	14	7	6	13	3								-
Nashville Warbler							91	91	84	94	70	74			-	-			-	-
Yellow Warbler[e]										3										
Yellow-rumped Warbler							29	40	31	53	16	41								
Black-throated Gray Warbler							85	91	84	79	73	77				-			-	-
Townsend's Warbler[g]	49	14	48	2	45	3	21	17	15	15	13	5		-				-		
Hermit Warbler							100	97	100	98	98	100			+	+			+	+
MacGillivray's Warbler							38	51	36	48	45	38				-			+	
Yellow-breasted Chat[e]							3	6		2										
Wilson's Warbler							52	57	50	73	55	82							+	
Northern Oriole[e]								9	2			3								

Table 3. Cont.

Species	Percent Frequency among Age Classes												Association with Stand Age[b]							
	Winter						Spring						ANOVA Test[c]				Correlation[d]			
	< 150		150-250		> 250		< 150		150-250		> 250		Winter		Spring		Winter		Spring	
	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82	81	82
Brown-headed Cowbird							6	14	8	2	3	3								
Western Tanager							100	97	98	100	96	100			-	-			-	-
Black-headed Grosbeak							100	100	98	97	100	100			-	-			-	
Lazuli Bunting[e]							3	9		10		3								
Evening Grosbeak	6	26		16	3	13	21	4	30	2	21	3		-				-		
Purple Finch	30	6	7	10	11	3	60	57	65	77	63	69	-				-			
Pine Siskin	44	20	37	15	38	3	74	97	71	79	58	72				-				-
American Goldfinch[e]	3							3												
Lesser Goldfinch[e]			2				18	14	16	3					-				-	
Red Crossbill	12		6	3	10			11	6	2	3	3								
Rufous-sided Towhee		6	2	2			26	23	23	13	11	13				-			-	
Dark-eyed Junco	14	14	13	8	13	13	100	91	91	95	56	87			-			-	-	-
Chipping Sparrow							21	9	10		8									
Fox Sparrow[e]		11	2	6	6	3				5	5	5								
Song Sparrow[e]	3	3	2	3			3	3	3	3										

[a]Bird names follow American Ornithologists' Union (1982).

[b]Significant positive (+) or negative (-) association; $p < 0.1$.

[c]Comparison of mean densities among 3 age class groups.

[d]Spearman Rank Correlation of density with stand age (n = 136 plots).

[e]Recorded primarily as transients or visitors from adjacent or specialized habitats.

[f]Due to difficulty in identification, some 1981 records may actually pertain to E. oberholseri.

[g]All Spring records are of migrants.

Twenty-eight species were considered to be transients or visitors from habitats other than old-growth Douglas-fir. An additional 20 species occurred on fewer than 10 percent of the 136 study plots, and these were considered too rare for further correlation analysis. In this report, only frequency data are presented; however, in discussions of habitat relationships and year-to-year variation, conclusions will be supported with actual density estimates.

During winter, 1982, the following 7 species occurred on >50% of the plots: Brown Creeper (96%), Golden-crowned Kinglet (92%), Winter Wren (85%), Chestnut-backed Chickadee (84%), Varied Thrush (72%), Steller's Jay (61%), and Common Raven (50%). In spring 1982, Western Flycatcher, Steller's Jay, Red-breasted Nuthatch, Solitary Vireo, Hermit Warbler, Western Tanager, Black-headed Grosbeak, and Dark-eyed Junco occurred on >90% of our plots. An additional 14 species were recorded on at least 50% of the plots.

Associations with Stand Age

Mean bird species richness and total density generally did not vary significantly among plots in the 3 age classes (Figure 1). The exception was in winter 1982 when we found fewer species in AC1 than in AC3, with AC2 being intermediate.

During the 4 seasons, we found 56 significant correlations between population density estimates and stand age, in 120 separate tests among 44 bird species (Table 3). This is many more than would be expected by chance ($p < 0.001$, Rohlf and Sokal 1969:212), strongly suggesting that species are not distributed at random with respect to age characteristics in Douglas-fir forests. However, interpreting individual bird species' associations with stand age is more difficult, due to their general inconsistency over the

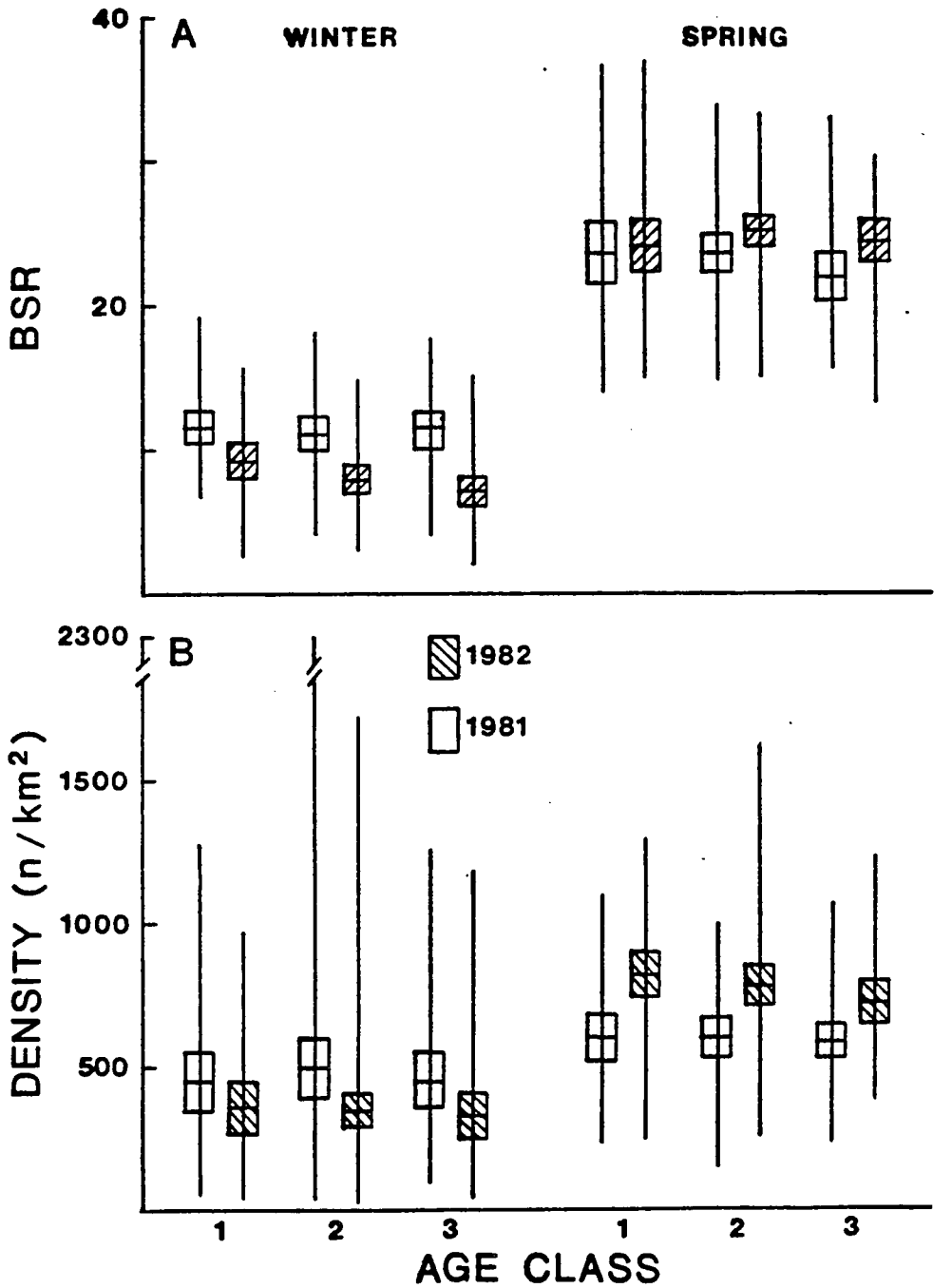

Figure 1. Comparison of (A): mean bird species richness (BSR) and (B): mean density estimate of birds among stand age classes in winter and spring, 1981 and 1982. Vertical lines indicate range, bars indicate 95% confidence interval. Stand age classes are: 1, <150 years; 2, 150-250 years; 3, >250 years.

four seasons of study.

Eighteen species were significantly ($p < 0.10$) more abundant in the oldest stands in at least one season, 4 in winter and 14 in spring (Table 3). Of these, Chestnut-backed Chickadee, Hermit Thrush, Golden-crowned Kinglet, Warbling Vireo, and Hermit Warbler were most abundant in older stands during both 1981 and 1982 breeding seasons. The other 13 species showed no interpretable pattern of abundance among the 4 seasons. Twenty-four species were significantly more abundant in the younger stands in at least one season. Eleven of these occurred over 2 or more seasons, 3 in winter, 8 in spring. Most species showing consistent negative associations with stand age characteristics belong to either of 2 groups. Some, such as Nashville Warbler, Lesser Goldfinch, and Rufous-sided Towhee, are generally more abundant in cutover or other open habitats and were frequently detected on the edges of our plots. Of the 28 species detected only as transients or visitors, 68% occurred only on the younger-aged plots (AC1, AC2).

Other species, such as Ruby-crowned Kinglet (winter), Solitary Vireo, Black-throated Gray Warbler, Western Tanager, and Black-headed Grosbeak, are forest inhabitants, but appear to select sites that have particular vegetation characteristics, notably many oak trees, more typical of younger Douglas-fir forests.

A few birds, such as American Robin, Hermit Thrush, and Golden-crowned Kinglet, were most abundant in older stands in spring and in younger stands in winter (Table 3). Whether this shift represents an influx of a separate population of birds in winter with different habitat preferences, or a seasonal change in preference by resident individuals, is impossible to determine at this time.

Year-to-Year Changes

Over the first 2 years of this study, we experienced a marked difference in weather on our plots, particularly in winter. This, in effect, was a natural experiment allowing us to test the importance of year-to-year variation relative to the population-habitat trends discussed above. In general, winter 1981 was relatively mild (average temperature = 9°C) and dry (total precipitation = 89 cm), with little prolonged snow cover on our plots. Winter 1982 was colder (average temperature = 7°C) and wetter (total precipitation = 137 cm), with snow cover lasting into March and early April. Bird activity noticeably declined during the cold winter, and several resident insectivorous species were unusually scarce throughout the region. Springs (May-June) were more similar in the 2 years.

Winter.--Between winter 1981 and 1982, 6 species occurred with higher frequency and 10 species decreased (Table 3). All of these changes in frequency paralleled changes in population density estimates, except in the case of the Hermit Thrush, discussed below.

Red-breasted Nuthatch, Ruby-crowned Kinglet, Hutton's Vireo, Townsend's Warbler, and to a lesser extent Chestnut-backed Chickadee, decreased markedly in 1982. The warbler was virtually absent from the area after January. It is possible that this species and the Ruby-crowned Kinglet (which both occur in winter only) staged a facultative migratory movement in response to the winter storms (Terrill 1981). Although it is likely that lower populations of the other, more sedentary, permanent residents reflect actual winter mortality, the large movement of nuthatches back into one study area in March suggests that local movements of these species can occur.

Winter Wren, another small insectivore, increased greatly in the cold winter, suggesting an influx of birds escaping an even harsher winter further north. Brown Creepers and Red-breasted Sapsuckers may have behaved similarly, though to a lesser extent. The other small insectivore of concern, Golden-crowned Kinglet, did not exhibit an overall population change between winters, although subsequent breeding levels appeared reduced in 1982 (see below).

The ground-foraging Northern Flicker and American Robin also decreased greatly in 1982, most likely due to increased snow area. An overall decline in numbers of Hermit Thrush and Varied Thrush (not statistically significant) was also part of this pattern. That Hermit Thrush was detected on more plots in 1982 was possibly due to our greater familiarity with this species' winter call notes compared to 1981 (i.e., we may have missed birds actually present in 1981).

Among the seed-eating fringillids, one increased (Evening Grosbeak) and 2 decreased (Pine Siskin, Red Crossbill) between the two winters. These are notoriously irruptive and erratic species, and population fluctuations should be expected.

Finally, the significant increase in Pileated Woodpecker numbers is of great interest because of this species' regional dependence on coniferous forests. However, this increase cannot be attributed to any particular climatic or habitat response at this time.

Overall, significantly fewer species were observed in winter 1982 than in 1981, across all age classes (Figure 1). Total density was also less in all age classes, although these differences were not statistically significant in any one class.

Spring.--Between spring 1981 and 1982, 10 species increased and 10 decreased in terms of frequency of occurrence on plots. Again, most changes were supported by concomitant changes in population density.

Total breeding density was significantly higher in 1982 in all age classes (Figure 1). Contributing most to this increase were many small summer resident, foliage-gleaning insectivores, in particular Warbling Vireo, Nashville, Yellow-rumped, MacGillivray's and Wilson's Warblers. In addition, Western Flycatcher and Black-headed Grosbeak, both occurring on nearly 100% of the plots in both years, increased significantly in density in 1982. Many of these species have breeding populations extending well to the north of our area, and pass through on their spring migration in May. As migrating individuals often sing at this time, it is impossible to discriminate between these and locally territorial residents with our censusing technique. Thus, we cannot accurately assess the degree to which some species actually increased their breeding densities on our study plots.

Among the permanent resident insectivores, Chestnut-backed Chickadee, Golden-crowned Kinglet, and Hutton's Vireo (all foliage gleaners) decreased significantly in both frequency of occurrence and breeding density in 1982 (Table 3). Red-breasted Nuthatch remained more numerous as breeders in 1982, following their return to our study area in March. Winter Wren also remained at a much greater density in spring 1982, after increased population levels the previous winter. Brown Creeper numbers were similar in the two breeding seasons. These latter 3 species are primarily bark or litter foragers. It is possible that higher densities of summer visitor, foliage gleaners were in part a response to lower densities of permanent residents potentially exploiting the same resources.

Among cavity-nesting species, Pileated Woodpeckers remained in significantly higher numbers in spring 1982, whereas Northern Flickers bred in significantly lower densities after their marked decline in winter 1982.

As expected, fringillid numbers continued to fluctuate with Pine Siskin and Evening Grosbeak reversing the trends they exhibited in winter. Densities of Purple Finch, a normally non-irruptive species, were identical in the two breeding seasons.

Conclusions

From the above discussions, it is apparent that year-to-year variation in bird populations can be great, and that these can seriously bias our assessment of species-habitat relationships. Overall, 36 species exhibited some significant relationship with stand age, and roughly 25 species showed significant year-to-year variation in numbers. Half of those species that varied in abundance also shifted their degree (statistical significance) or direction (positive or negative) of association with stand age between years. The possible confounding effects of such variation on the age relationship is exemplified by the American Robin. In the mild winter of 1981, when Robins were numerous, they occurred most frequently and in highest density in the oldest stands (positive correlation with age). In the cold winter of 1982, Robins were rare and occurred primarily in the youngest stands (negative correlation). Their breeding density was negatively correlated with stand age in both years, but their winter stand age preference reversed over the 2 years. Any conclusion about the habitat requirements of this species based on a single season or even a single year's data would be misleading.

Nevertheless, consistent patterns are beginning to emerge. In particular,

we feel that a distinct bird community does exist in old-growth Douglas-fir forests (AC3), especially in the breeding season. This community includes high densities of those species showing consistent positive associations with stand age, namely Chestnut-backed Chickadee, Hermit Thrush, Golden-crowned Kinglet, Warbling Vireo, and Hermit Warbler.

We used discriminant analysis to test the relative distinctness of the bird communities in each age class based on abundance of each bird species in 2 seasons and 2 years. For comparison, we also performed a discriminant analysis using only the vegetation characteristics. Results show that AC1 and AC3 were distinct for all comparisons (Table 4). Similarly, AC1 and AC2 were consistently distinct. Comparisons of AC2 and AC3 revealed significant differences only for analyses of spring birds and vegetation; winter bird abundances in AC3 and AC2 were not significantly different (Table 4).

Our analysis of bird species-stand age correlations must be viewed as preliminary. In particular, the effects of other variables such as elevation and specific vegetation characteristics may cloud simple relationships with stand age. These will be the focus of our analysis in the coming year. The exact requirements of bird species in Douglas-fir forests may be further elucidated by examining their specific foraging behaviors. This will be discussed in detail in the following section.

Avian Foraging Behavior

During the period January-March 1982, 350 observations of 13 species were made. Sample sizes for 3 common species (Chestnut-backed Chickadee, Brown Creeper, and Golden-crowned Kinglet) were sufficient to allow detailed analysis. These 3 species comprise a large proportion of the small

Table 4. Results of discriminant analyses comparing stand age classes using vegetation features and bird abundances.

Analysis	R^2[a]	Classification success (%)[b]	Pairwise Comparisons[c]		
			1 vs 2	1 vs 3	2 vs 3
Vegetation[d]	0.51	58	1.23***	2.53***	1.30***
Winter '81 birds[e]	0.35	55	1.34***	1.03**	0.31
Spring '81 birds[e]	0.57	71	1.34**	2.23***	1.94***
Winter '82 birds[e]	0.29	53	1.25***	1.46***	0.21
Spring '82 birds[e]	0.60	74	1.86***	2.20***	1.66***

[a]Proportion of total variance explained.

[b]Percentage of plots correctly classified using discriminant functions (same plots used to derive functions).

[c]Values for each comparison are Euclidian distances between mean discriminant scores of each age class. Significance tested using multivariate F-test (*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, blank = $p \geq 0.05$. Sample sizes: 1 (<150) = 35, 2 (150-250) = 62, 3(>250) = 39.

[d]Variables from Table 2, except litter and duff depth.

[e]Only those species found on at least 10% of plots included in analysis.

insectivorous birds in the winter forest, and population data show the chickadee and kinglet declined significantly after the cold winter period.

All fed primarily by gleaning insects off various surfaces, although the chickadee occasionally pecked at wood to expose hidden prey (Figure 2A). The creeper fed almost exclusively from bark, whereas the chickadee and kinglet fed largely on foliage substrates (Figure 2B). The kinglet used mosses and lichens to a greater extent than the other two.

All 3 species were observed in Douglas-fir trees about 50-60% of the time (Figure 2C). Creepers and kinglets also fed on oaks to a large extent, whereas chickadees were observed frequently (17%) in Pacific madrones and in a wide variety of other trees. As for portion of tree used (Figure 2D) creepers stayed on or very close to the main trunk whereas the others fed mostly in the outer shell of leaves or twigs.

Kinglets and creepers were observed most frequently in the lower canopy layer (0-10 m) and the mid-canopy layer (11-20 m); only the chickadee was regularly observed above 20 m (Figure 2E). Chickadees appeared to use trees in the 3 size classes rather equally (Figure 2F). Creepers were observed more frequently in medium diameter trees, whereas kinglets used smaller trees ($\leq$ 53 cm) most often.

Using Euclidian distance (ED) as a measure of similarity, we found the kinglet and chickadee were most alike in their foraging (ED = 25), with the creeper being quite divergent (ED = 39 from kinglet, 54 from chickadee). These findings are consistent with studies of these and similar species in other temperate forests. It is generally assumed that divergent foraging behaviors have evolved in response to periodic food shortages which undoubtedly occur during some or most winters. Further

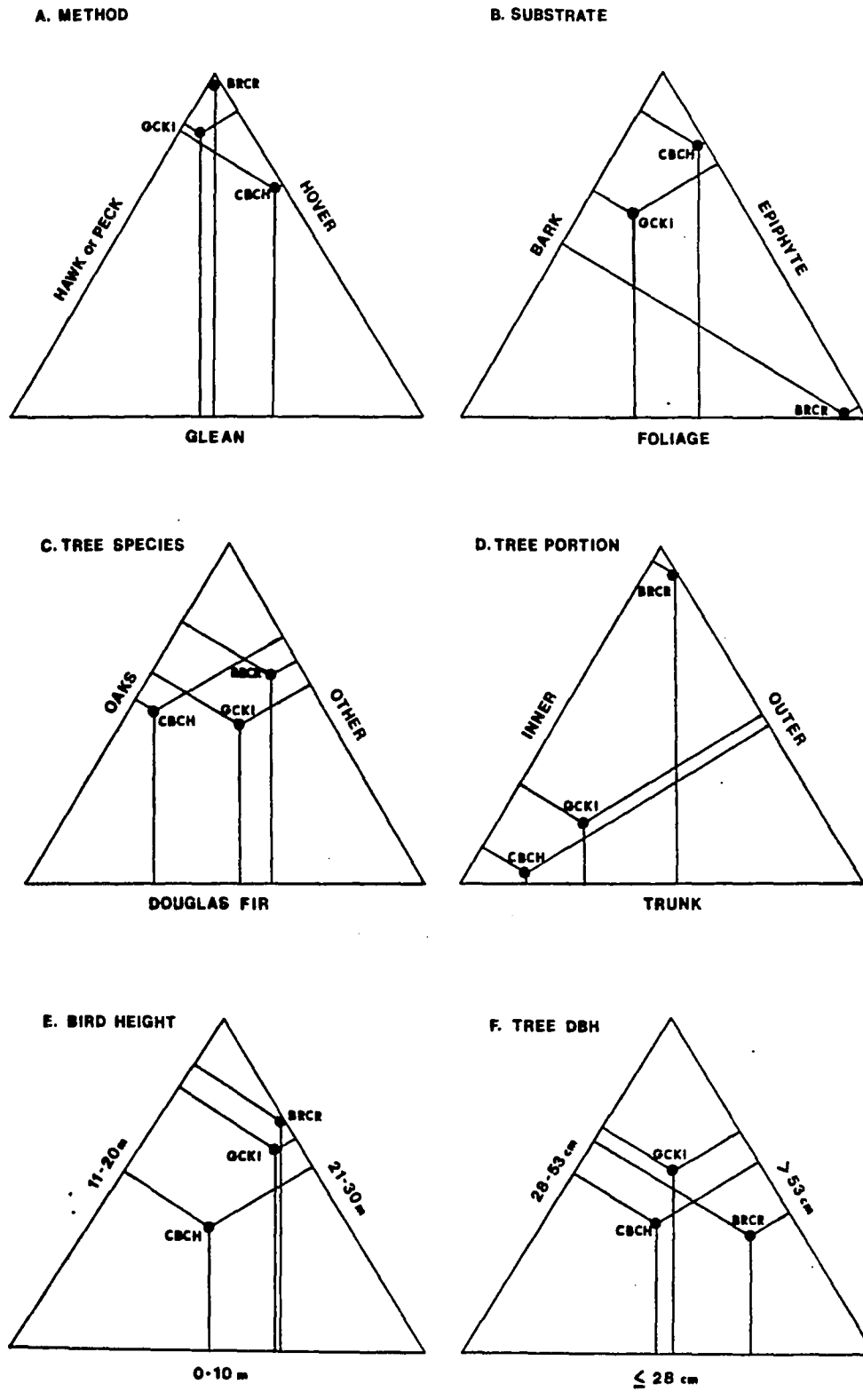

Figure 2. Foraging behavior of 3 insectivorous bird species, January-March 1982, in relation to (A) Method, (B) Substrate, (C) Tree species, (D) Tree portion, (E) Foraging height, and (F) Tree EBH. Species and sample sizes are Chestnut-backed Chickadee (CBCH, n = 71), Brown Creeper (BRCR, n = 94), and Golden-crowned Kinglet (GCKL; n = 96). In each diagram, the percentage of observations is represented by a line perpendicular to the labelled side of the triangle. The relative positions of species within a triangle are proportional to Euclidian distance calculated from actual percentage data.

study is needed to determine what components of Douglas-fir forests contribute most to winter survival in these and other bird species.

Additional foraging observations were made during May and August 1982. About 270 observations of 25 species were collected, although samples for any single species were small. In May, where bird activity was highest, we found it very difficult to collect foraging data within our busy bird censusing and pitfall monitoring schedule. In August, when more time was available, bird activity was extremely low. At that time we were able to test various modifications of our techniques, modeled after those of C. J. Ralph (pers. comm.).

Although we cannot meet our first 2 objectives with the data collected thus far, we feel we can incorporate a modified observation approach more efficiently into the fieldwork during the coming year. Fulfilling these goals is necessary to tie certain species more closely to the habitat characteristics identified during other phases of this study.

Owl Populations

During the nighttime censusing in 1982, 25 owls of 4 species were detected. Spotted Owls were heard at 16 study plots, Western Screech Owls at 5 plots, Saw-whet Owls at 3 plots, and a Great-horned Owl at one (Table 5). Compared with the 1981 census, we found about the same number of Spotted and Saw-whet Owls, but many fewer Screech Owls. This difference may be attributable to the early timing of the 1982 census or to a scarcity of owls in response to severe winter conditions in March. The reason for the paucity of the Saw-whet Owl detections is still unclear.

If information from diurnal bird census, field notes, and the efforts of other owlers in our area are combined with our owl census, we can assemble a more complete picture of the distribution of owls on our

Table 5. Owls recorded during nighttime censuses in 1981 and 1982. Values are proportion of plots on which owls occurred within each stand age class.

Species	1981			1982		
	< 150	150-250	> 250	< 150	150-250	> 250
Screech Owl	0.37	0.11	0.13	0.10	0.02	0.09
Flammulated Owl	0	0.04	0			
Spotted Owl	0.11	0.13	0.22	0.05	0.24	0.18
Saw-whet Owl	0	0.07	0.09	0	0.02	0.09
Great-horned Owl				0	0	0.05

plots (see Table 5). Spotted Owls were consistently detected more frequently in AC2 and AC3 than in AC1, but this trend was not statistically significant in either year ($p = 0.20$, Chi-square). Though rarely detected in both years, Saw-whet Owls only occurred in AC2 and AC3. Screech Owls were much more widespread in AC1 in 1981, but 1982 records were too few to confirm this trend. Northern Pygmy Owls were primarily detected during daytime fieldwork; they seemed to be evenly distributed among the 3 age classes.

Squirrel Census

During the winter and spring bird censuses, we also censused 3 squirrel species: Allen's Chipmunk, Western Gray Squirrel and Douglas' Squirrel (see Table 10 for scientific names). Average density estimates for these species ranged from 0.2, 0.8, and 1.7 per 100 ha in winter to 3.3, 1.7, and 14.0 in spring, respectively (Figure 3). Densities were generally lower than in 1981. The density estimate of Allen's Chipmunk increased with stand age in spring for both 1981 and 1982 (Figure 3A). Western Gray Squirrel abundance was negatively correlated with age in spring 1981 but the trend was not significant for spring 1982 (Figure 3B). Douglas' Squirrel density estimates were consistently highest in AC2.

Winter density estimates were significantly lower in 1982 for the Douglas' Squirrel; spring densities did not differ (Figure 3C). This suggests that the apparent winter decline may reflect reduced detectability rather than an actual change in numbers. Douglas' Squirrels cache food and retreat to underground nests during severe weather (Maser et al. 1981). Thus, these squirrels may have spent more time in nests in winter 1982 compared with 1981. Density estimates of Allen's Chipmunk and Western Grey Squirrel did not differ between years.

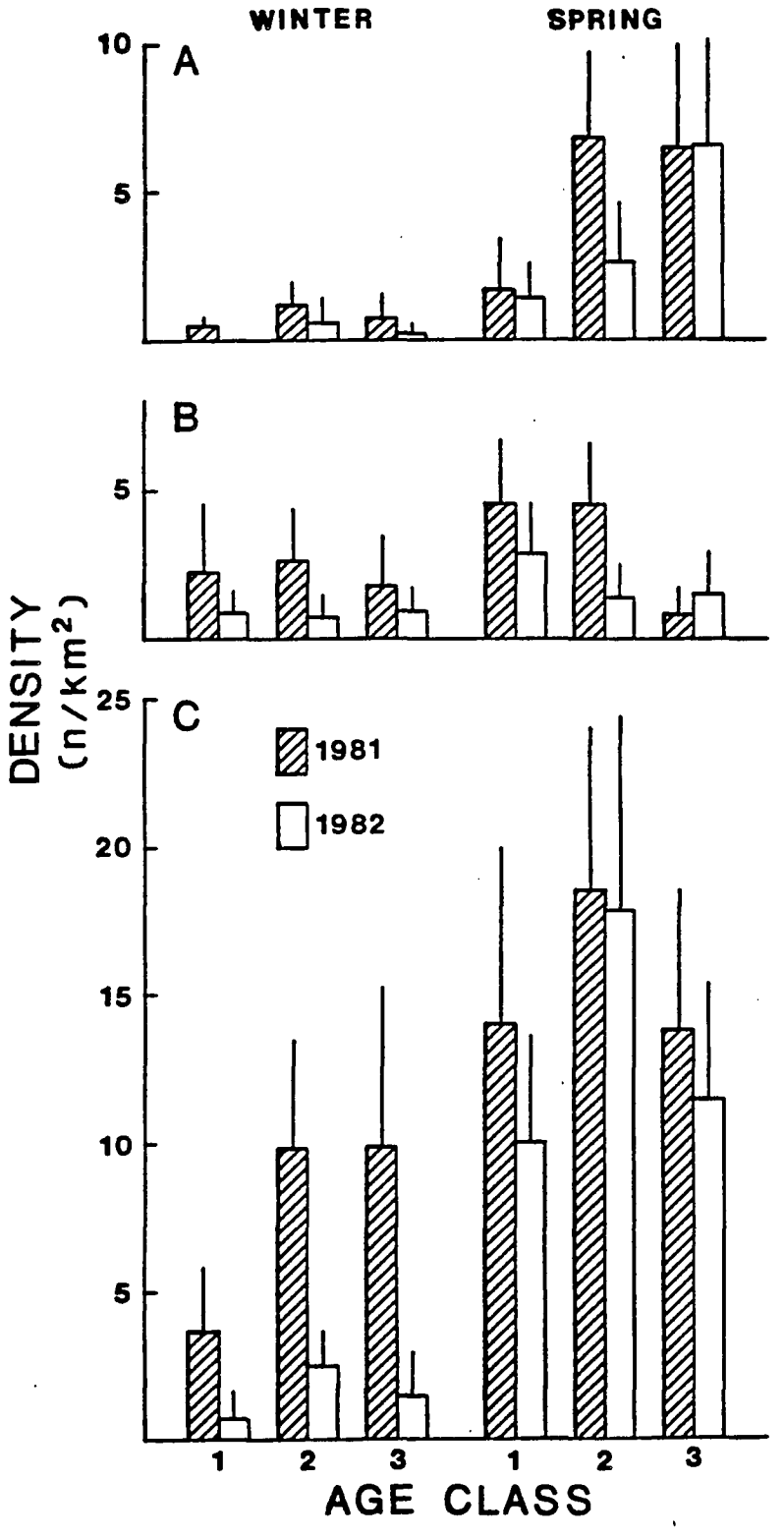

Figure 3. Mean density of (A) Allen's Chipmunk, (B) Western Gray Squirrel, and (C) Douglas' Squirrel in relation to stand age class, year, and season. Counts derived from variable circular plot census.

Pitfall Traps

We captured a total of 2,608 animals in 1,340 pitfall traps between October 1981 and September 1982 (Table 6). Nine of the 25 species were mammals (1,448 individuals), 10 were amphibians (625 individuals), and 6 were reptiles (535 individuals). Shrews, the most frequent animal captured (35% of total), were captured in equal proportions among age classes in all 3 trapping periods. However, the winter capture rate on individual plots was positively correlated with stand age.

Shrew-moles also showed no difference in capture rate among age classes. Western Red-backed Voles were found in significantly greater numbers in the oldest stands during winter. During that season, we captured 126 of the 167 voles recovered over all periods. The combined capture rate from the 3 periods was positively correlated with stand age. Abundant cover and dead woody material that are important habitat requirements for this vole (Maser et al. 1981) are found in greater quantity in the older stands (Table 2). Other mammals caught in greater numbers in older stands included Deer Mouse (winter), Pacific Shrew (spring), and Coast Mole.

Among reptiles and amphibians, Ensatina was captured with highest frequency (21% of all captures; see Table 10 for scientific names). Capture rates were significantly higher in older plots during the summer period but did not differ among age classes in the other periods (Table 6). However, captures on individual plots were positively correlated with plot age in all sample periods. This species requires a moist substrate for respiration (Stebbins 1954). Older stands are characterized by greater duff depth and downed wood (Table 2). In summer, it is likely that moisture may limit movement of Ensatina; the greater cover provided by older stands may create

Table 6. Pitfall capture rates (n/1000 trap nights)among stand age classes for each season during 1982.

Species[d]	Winter[a]				Spring[b]				Summer[c]				Total	
	< 150	150-250	> 250	Corr.[e]	< 150	150-250	> 250	Corr.	< 150	150-250	> 250	Corr.	Captures	Corr.
Pacific Giant Salamander	0.00	0.00	0.07						-	-	0.06		4	
Northwestern Salamander	0.03	-	-										1	
Rough-skinned Newt	0.14	0.11	0.05		0.03	0.05	-						18	
Del Norte Salamander	-	0.19	0.23		-	0.06	-		-	0.06	-		26	
Ensatina	2.57	3.77	2.96	+	0.60	1.79	1.74	+	0.03	0.40	0.94[f]	+	545	+
Black Salamander	0.03	0.04	-										3	
Clouded Salamander	0.03	-	-										1	
Western Toad	0.11	0.07	-		0.07	0.10	0.06						15	
Pacific Treefrog	0.09	-	-		-	0.08	-						9	
Western Fence Lizard	0.09	0.03	-		2.65	1.10	0.03	-	1.18	0.34	1.04	-	147	-
Sagebrush Lizard	-	0.08	-		0.09	0.13	-		0.14	0.08	0.04		19	
Western Skink	0.14	0.09	0.08		0.31	0.82	0.09		3.19	0.80	0.28	-	144	-
Southern Alligator Lizard	-	-	0.02		0.64	0.20	0.09	-	0.09	0.11	-		32	-
Northern Alligator Lizard	0.06	0.11	0.03		0.77	0.48	0.75		1.75	1.58	1.08	-	190	
Sharp-tailed Snake	0.03	-	-						-	0.02	0.05		3	
Shrew spp[g]	2.90	2.80	3.53	+	3.95	4.08	3.90		1.84	2.91	3.15		903	
Pacific Shrew	0.13	0.05	0.17		-	0.08	0.32						25	

Table 6. Cont.

Species[d]	Winter[a]			Corr.[e]	Spring[b]			Corr.	Summer[c]			Corr.	Total Captures	Corr.
	< 150	150-250	> 250		< 150	150-250	> 250		< 150	150-250	> 250			
Shrew-mole	0.78	0.69	0.82		1.37	1.12	1.32		0.11	0.12	0.22		221	
Coast Mole	-	0.09	0.08		-	0.08	0.07		-	-	0.12		17	+
Deer Mouse	0.03	0.37	0.62	+	0.12	0.27	0.04		0.11	0.40	0.20		85	
Pinyon Mouse	0.12	0.05	0.22		0.07	0.02	0.08		-	0.07	0.03		25	
Western Red-backed Vole	0.78	0.74	1.44	+	0.20	0.53	0.39		-	0.05	0.06		169	+
Pacific Jumping Mouse									-	0.04	0.04		2	
Olympic Salamander					-	0.06	-						3	
Short-tailed Weasel	-	0.01	-										1	

[a]Sample sizes: < 150 = 34, 150-250 = 61, > 250 = 39; total trapnights = 127,869.

[b]Sample sizes: 150 = 35, 150-250 = 61, 250 = 39; total trapnights = 102,049.

[c]Sample sizes: 150 = 35, 150-250 = 60, 250 = 38; total trapnights = 73,081.

[d]See Table 10 for scientific names.

[e]Spearman Rank Correlation with stand age (n = 136 plots); +, positive; -, negative.

[f]Underlined values differ significantly ($p < 0.10$, F-test).

[g]Includes *Sorex trowbridgii*, *S. vagrans*.

moister conditions in the understory compared to younger stands.

The Western Fence Lizard, Western Skink, and Southern Alligator Lizard were caught at significantly higher rates in younger stands during their periods of highest abundance (Table 6). Northern Alligator Lizard abundance was equal among age classes, but was negatively correlated with plot age in summer. These species all depend on drier, warmer sites for thermoregulation; younger stands provide these sites more predictably than older stands.

To compare the relative productivity of pitfall trapping sessions, we computed the number of records of species-presence on each plot over each trapping period. As shown in Figure 4, we continued to accumulate records even during the last session, although at a declining rate. Total records in each session were approximately equal, but spring sampling was most productive. Considering the number of trapnights accumulated in each session, it is apparent that summer, 1981 was most productive (27 records per 1000 trapnights compared with 2-4 records per 1000 trapnights in other periods.

The summer periods of 1981 and 1982 allow an assessment of water-filled and baited versus dry pitfall traps. Although total presence records were about equal in the 2 years (Figure 4), traps were open 7 times longer in 1982. The higher rate of success of wet, baited traps in 1981 was offset by the more frequent damage by bears and the increased human effort required for maintenance. We conclude, therefore, that unbaited, dry traps, remaining open for a longer time period, provide the most efficient sampling design.

Track Stations

In summer 1982 we detected tracks of 14 mammal taxa on 135 plots (Table 7).

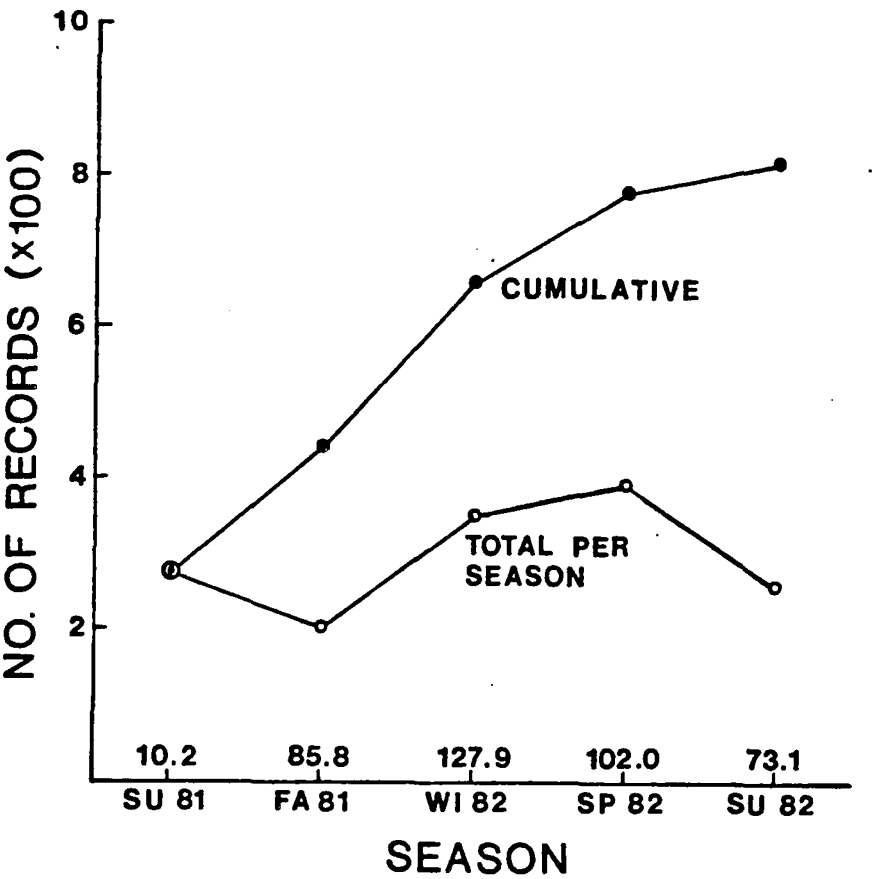

Figure 4. Species-occurrence in relation to season from pitfall captures. Values above seasons indicate thousands of trapnights for each season.

Table 7. Frequency of occurrence of mammals on plots as recorded on track stations, for 1981 and 1982. Values are proportions of all plots in each age class on which a species was recorded.[a]

Species	1981 < 150 (n=35)	1981 150-250 (n=61)	1981 > 250 (n=39)	Correlation[b]	1982 < 150 (n=35)	1982 150-250 (n=61)	1982 > 250 (n=39)	Correlation[b]
Chipmunk species[c]	54.3	27.9	48.7		8.6	24.6	30.8	+
Western Gray Squirrel	20.0	13.1	-	-	5.7	14.8	7.7	
Douglas' Squirrel	17.1	23.0	33.3	+	2.9	26.2	23.1	
Northern Flying Squirrel					11.4	18.0	12.8	
Dusky-footed Woodrat	2.9	18.0	10.3		2.9	4.9	20.5	+
Coyote	8.6	4.9	2.6		-	1.6	-	
Gray Fox	37.1	4.9	10.3	-	25.7	18.0	2.6	-
Black Bear	28.6	60.7	41.0		42.8	42.6	38.5	
Ringtail	17.1	6.6	7.7	-	8.6	4.9	2.6	
Raccoon	-	1.6	-					
Fisher[d]	8.6	18.0	20.5		8.6	6.5	20.6	
Long-tailed Weasel	2.9	4.9	2.6		-	-	2.6	
Mink	2.9	6.6	-					
Spotted Skunk	25.7	24.6	20.5		-	9.8	20.5	+
Striped Skunk	8.6	9.8	-		-	6.6	-	
Bobcat	2.9	-	-		5.7	-	-	

[a]The probability that proportions are equal among strata was tested by X^2 (underlining denotes $p < 0.10$). X^2 was not calculated for species with low detection rates.

[b]Spearman's correlation coefficient, $p < 0.10$. (+) denotes positive correlation with age while (-) denotes negative correlation.

[c]Chipmunk species includes Northern Flying Squirrel for 1981 due to track misidentification.

[d]These may include up to 3 Marten (Martes americana). Tracks of Marten and Fisher are very similar except that Fisher tracks average about 20% larger. The few questionable records could have been either juvenile Fisher or adult Marten. We have retained tape impressions of these tracks and will consult with other experts to verify identifications.

These included 4 squirrels, Dusky-footed Woodrat, 2 canids, Ringtail, Black Bear, 4 mustelids, and Bobcat. Black Bear was detected most frequently, followed by Chipmunk, Douglas' Squirrel, Gray Fox, and Northern Flying Squirrel. Douglas' Squirrel, Dusky-footed Woodrat, and Spotted Skunk occurred significantly more often in AC3 plots while number of Gray Fox records was greatest for AC1 plots.

Two species, detected rarely last year, were not observed this year (Raccoon, Mink). Northern Flying Squirrel were recorded this year but not last year, primarily because of misidentification last year (improperly identified as chipmunks). All other species were recorded both years, but total frequencies and relative occurrence in age classes differed between years (Table 7).

Of the 14 species that were consistently identified in either year, 8 showed significant trends with stand age. Chipmunks, Douglas' Squirrel, Dusky-footed Woodrat, Black Bear, and Spotted Skunk occurred more frequently in older age classes in at least one year. Douglas' Squirrel was the only one that showed a significant trend in both years. Dusky-footed Woodrat occurred most frequently in older stands in both years but this trend was not significant in 1981 (Table 7). Although Fishers occurred more frequently in older stands each year, only when records for both years were combined was this trend significant (see Table 10).

Western Gray Squirrel, Gray Fox, and Ringtail were negatively associated with stand age in at least one year. Only Gray Fox was consistently found in young stands over both years. The negative trend for Gray Squirrel in 1981 was consistent with census data for spring 1981. It feeds on acorns of many oak species (Maser et al. 1981); its higher abundance in young

Table 8. The average number of animals captured per plot by live trapping in each 3 age classes of Douglas-fir forest, 1981 and 1982.

Species	< 150[a]		150-250[a]		> 250[a]		Significance[b]	
	81	82	81	82	81	82	81	82
Shrew species[c]	2.7	3.8	0.9	5.2	1.3	5.0		
Shrew-mole	0	0.5	0	0.3	0	0.4		
Western Red-backed Vole	1.0	0.5	2.3	2.0	1.5	1.2		
Dusky-footed Woodrat	4.0	1.3	4.7	2.8	15.4	3.3		
Deer Mouse	5.0	1.0	20.0	13.4	19.0	13.1	+	+
Pinyon Mouse	12.0	5.8	2.3	2.0	15.5	6.5		
Northern Flying Squirrel	0.7	2.0	0.3	0.4	0	1.3		
Allen's Chipmunk[d]	0.3	0.5	5.1	6.5	4.5	10.3		+
[redacted]tal	25.7	15.3	35.8	32.6	56.9	40.9	+	+
Population estimate	31.0	21.3	48.4	60.0	105.5	68.5	+	+
Estimated Density	7.2	3.5	9.7	12.6	28.1	14.4	+	+

[a]Sample sizes for 1981: < 150 = 3, 150-250 = 10, > 250 = 2; 1982: < 150 = 4, 150-250 = 10, > 250 = 4. Captures were weighted for 4 plots having grids with < 100 traps.

[b]Significance of correlation (Pearson product-moment) of capture rates and actual stand age-index using each plot (1981, n = 15; 1982, n = 18). A "+" indicates a significant correlation ($p < 0.10$).

[c]Includes Sorex trowbridgii, S. vagrans.

[d]May include a small number of Sonoma chipmunks (Eutamias sonomae). Identification of voucher specimens is pending laboratory analysis.

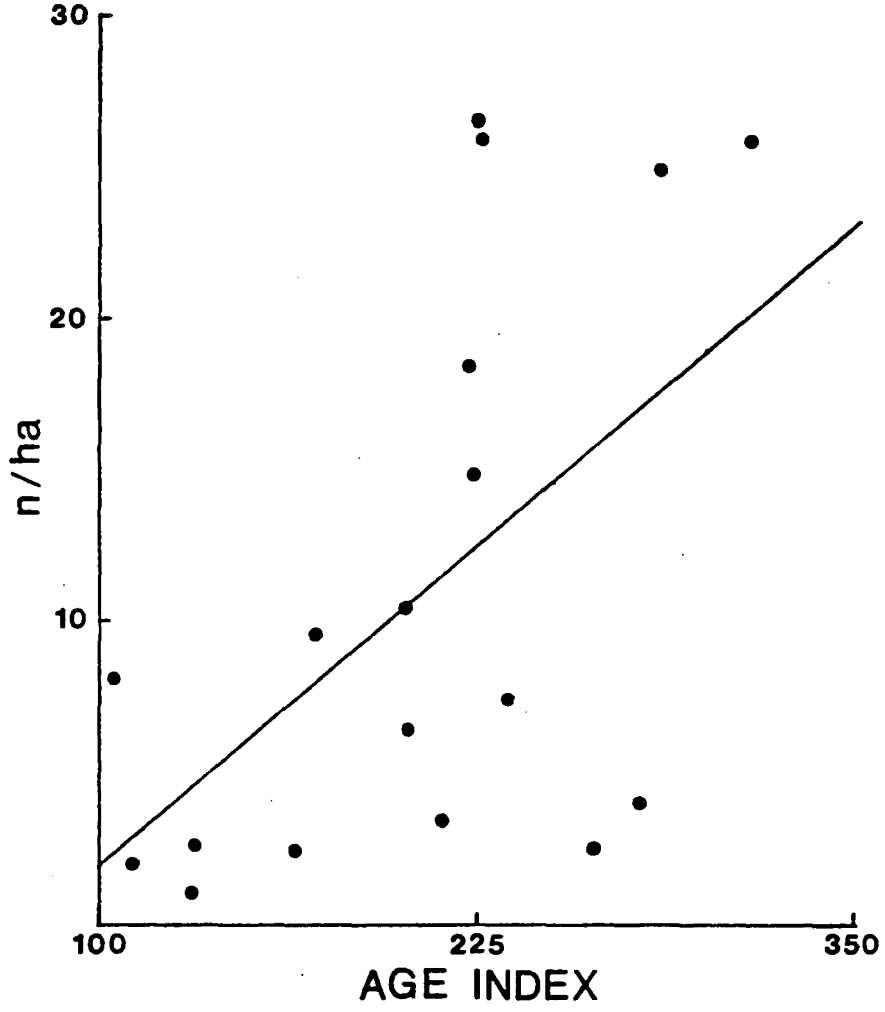

Figure 5. Density estimates of small mammals (all species) in relation to stand age, 1982 (n = 18 plots). Line is based on linear regression (r = 0.53).

not statistically significant. Habitats where this species was found typically included a large volume of dead and down material, a brushy understory, and mast-producing oaks.

The Western Red-backed Vole was captured more frequently in AC3 and AC2 compared with AC1. Although not statistically significant, this general trend was repeated in both years. Like many other small mammals, these voles use downed logs for nesting and cover.

Of the 7 species live-trapped in both years, 2 exhibited significant decreases in numbers from 1981 to 1982, while 1 increased significantly (Wilcoxon's signed-ranks test $p < 0.05$, Table 8). Deer Mouse decreased from 242 to 157 captures on the 15 grids trapped in both years while Dusky-footed Woodrat decreased from 81 to 42 captures. In addition, Pinyon Mouse exhibited a similar (although not significant trend), declining by 30%. Perhaps the severity of winter 81-82 decreased the availability of seeds and other food resources to overwintering mice. For whatever reason, there was a decline of nearly 50% in small mammal biomass in 1982. Shrews increased significantly from 19 captures in 1981 to 79 captures in 1982. This increase is difficult to explain, but because insectivores forage in duff, litter, and soil their prey resources may not have been as severely restricted as those of other small mammal species by the harsh 1982 winter.

Capture rates of 2 sciurids also increased in 1982, although neither increase was significant. Chipmunks increased on 9 of the 12 plots on which they were found, whereas the Northern Flying Squirrel was caught in higher numbers on 8 of 11 plots.

Intensive Herpetofauna Search

A total of 246 individuals representing 11 species were captured during

our intensive search on 27 plots. Most captures were amphibians (n = 243, 8 species). Only 3 reptiles were captured (3 species), but this was not surprising considering the time that searching took place (late fall). Four species comprised 96% of the captures: Ensatina, 68% (n = 167); Del Norte Salamander, 18% (n = 43); Clouded Salamander, 8% (n = 19), and Pacific Treefrog, 2% (n = 6).

Total captures were higher than expected in AC1 and AC2 (Chi-square, $p < 0.05$). We found 32 animals in AC1 stands (n = 4), 187 animals in AC2 (n = 18), and 27 in AC3 (n = 5). Mean capture rates were also highest in AC1 and 2 (Table 9). These differences were due almost entirely to Ensatina; capture rates of this species were greatest in AC1 and AC2 stands (Table 9).

These Ensatina data are in conflict with the pitfall results where Ensatina capture rates were positively correlated with stand age. Due to the large number of captures obtained from pitfall traps, the association of Ensatina with old growth stands is assumed to be correct. However, Ensatina seem to be patchily distributed with large numbers in relatively small patches of suitable habitat. Thus, it may be that young stands, which offer poor Ensatina habitat in general, may contain scattered patches of suitable habitat. For example, Ensatina density was not correlated with stand age, but was correlated with the volume of total downed woody material present ($r = 0.43$, $p < 0.05$, Figure 7), which is generally greater in older stands. Therefore areas with large volumes of downed material may provide suitable habitat regardless of stand age.

Table 9. Mean number of individuals and frequency of herpetofauna captured by stand age class during intensive litter search, fall 1981.

Species	< 150 (n = 4)		150-250 (n = 18)		> 250 (n = 5)	
	No./plot	Freq.[a]	No./plot	Freq.	No./plot	Freq.
Northwestern Salamander			0.1	6		
Pacific Giant Salamander			0.1	6		
Rough-skinned Newt	0.3	25	0.2	11		
Del Norte Salamander			1.9	33	1.6	40
Ensatina	6.5	100	7.0	94	3.0	100
Black Salamander			1.0	50	0.2	20
Clouded Salamander			0.1	6	0.2	20
Pacific Treefrog	1.3	50	0.1	6		
Western Fence Lizard					0.2	20
Northern Alligator Lizard					0.2	20
Southern Alligator Lizard			0.1	6		
All species	8.1		10.6		5.4	

[a]Percent of searched plots (3 subplots per plot) on which a species was found.

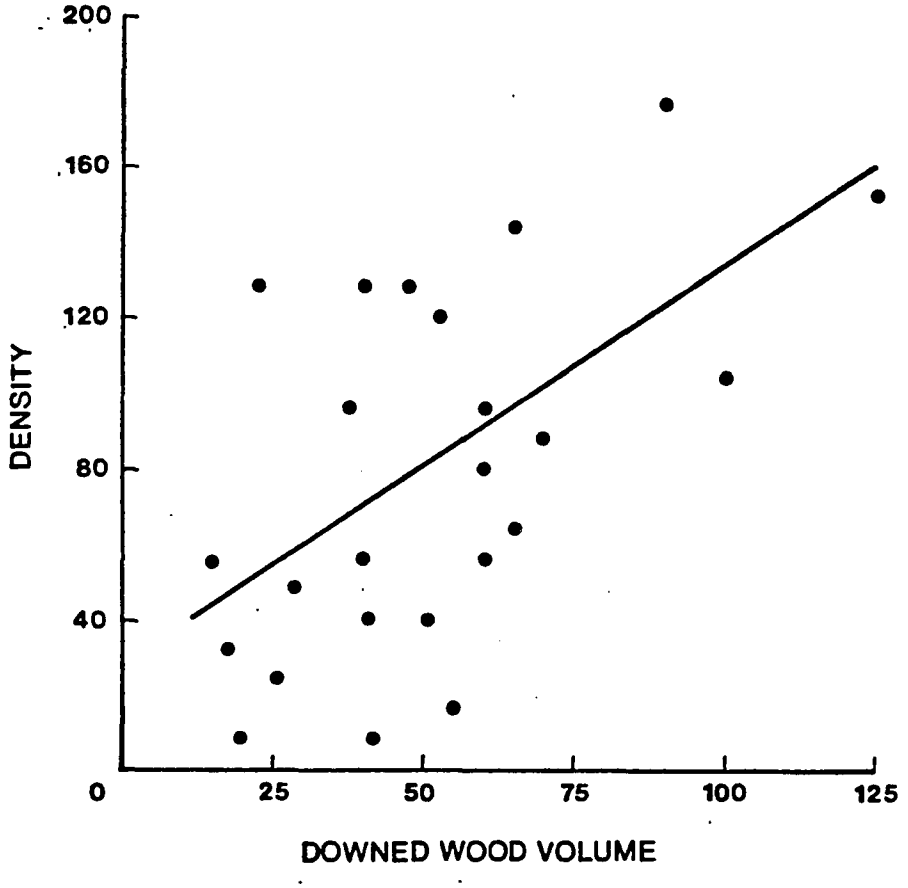

Figure 6. Salamander density (individuals per ha) in relation to downed wood volume (metric tons per ha). Line is based on linear regression ($r = 0.45$).

CONCLUSIONS

Having completed 2 full years of field sampling, we can now state with confidence that there are differences in both vegetation and wildlife among the 3 stand age classes we recognize. We believe that our age-index classification reflects differences in characteristics of old-growth compared to mature or sawtimber stands. These differences, exemplified by the results of the discriminant analyses described in Table 4, are most apparent between the oldest and youngest age classes.

We have summarized all bird observations over the 2 years in Table 3. Amphibian, reptile, and mammal records from both years are presented in Table 10, along with a chi-square analysis of the frequency data over the 2 years. Based on the data and tests from these 2 summary tables, plus the results of the individual analyses, we have compiled a list of species (Table 11) that show evidence of either a strong positive or negative association with stand age. Species on this list include only those captured or otherwise observed with sufficient frequency to allow an evaluation of the statistical significance of a relationship. Several other species revealed patterns of occurrence that, while suggesting an association, could not be supported statistically. These species include Pacific Giant Salamander, Del Norte Salamander, Spotted Owl, Screech Owl, and Hammond's Flycatcher. The Spotted Owl has been intensively studied in this geographical area; we suggest however that further intensive study is needed on all of these species.

Where we repeated the same sampling procedures in 1981 and 1982, we found considerable year-to-year variation in species abundance and, perhaps more significantly, in patterns of association with stand age. This underscores our belief that multi-year studies are of critical importance.

Table 10. Cumulative frequency of amphibians, reptiles and mammals recorded in 3 age classes of late-successional Douglas-fir forests in northwestern California, 1980-1982. Values are percentages based on all available data, from all sampling methods combined. Mammal names follow Williams (1979); amphibian and reptile names follow Stebbins (1966).

Species	Stand Age, Years[a]		
	< 150	150-250	> 250
AMPHIBIANS			
Northwestern Salamander *Ambystoma gracile*	3	3	
Pacific Giant Salamander *Dicamptodon ensatus*		6	10
Olympic Salamander *Rhyacotriton olympicus*	3		3
Rough-skinned Newt *Taricha granulosa*	9	16	3[b]
Del Norte Salamander *Plethodon elongatus*		26	13
Ensatina *Ensatina eschscholtzi*	86	84	100
Black Salamander *Aneides flavipunctatus*	3	16	3
Clouded Salamander *Aneides ferreus*	3	5	13
Western Toad *Bufo boreas*	11	8	
Pacific Treefrog *Hyla regilla*	43	24	10
Foothill Yellow-legged Frog *Rana boylei*	3	2	
Bullfrog[c] *Rana catesbeiana*	3		
REPTILES			
Pacific Pond Turtle *Clemmys marmorata*		2	
Western Fence Lizard *Sceloporus occidentalis*	69	32	8

Table 10. Cont.

Species	Stand Age, Years[a] < 150	150-250	> 250
Sagebrush Lizard *Sceloporus graciosus*	26	26	8
Western Skink *Eumeces skiltonianus*	63	40	15
Southern Alligator Lizard *Gerrhonotus multicarinatus*	34	18	8
Northern Alligator Lizard *Gerrhonotus coeruleus*	74	73	69
Rubber Boa *Charina bottae*		2	
Ringneck Snake *Diadophis punctatus*	3		
Racer *Coluber constrictor*	6	3	
Common Kingsnake *Lampropeltis getulus*	3		
Common Garter Snake *Thamnophis sirtalis*		5	5
Western Terrestrial Garter Snake *Thamnophis elegans*		2	5
Northwestern Garter Snake *Thamnophis ordinoides*			3
Western Rattlesnake *Crotalus viridis*			5
Sharp-tailed Snake *Contia tenuis*	3	2	3
MAMMALS			
Shrew species[d] *Sorex* spp	94	98	97
Pacific Shrew *Sorex pacificus*	12	11	23
Shrew-mole *Neurotrichus gibbsii*	63	56	56
Coast Mole *Scapanus orarius*	26	24	15

Table 10. Cont.

Species	Stand Age, Years[a]		
	< 150	150-250	> 250
Brush Rabbit *Sylvilagus bachmani*		2	
Allen's Chipmunk[e] *Tamias senex*	71	77	85
Western Gray Squirrel *Sciurus griseus*	57	62	33
Douglas' Squirrel *Tamiasciurus douglasii*	83	95	97
Northern Flying Squirrel[c] *Glaucomys sabrinus*	14	24	15
Deer Mouse *Peromyscus maniculatus*	54	66	59
Pinyon Mouse *Peromyscus truei*	60	43	33
Dusky-footed Woodrat *Neotoma fuscipes*	26	31	38
Western Red-backed Vole *Clethrionomys occidentalis*	40	53	69
Red Tree Mouse *Arborimus longicaudus*		2	
Pacific Jumping Mouse *Zapus trinotatus*		2	3
Porcupine *Erethizon dorsatum*		2	
Coyote *Canis latrans*	11	11	13
Gray Fox *Urocyon cinereoargenteus*	51	27	13
Black Bear *Ursus americanus*	57	85	64
Ringtail *Bassariscus astutus*	23	10	10
Raccoon *Procyon lotor*	3	5	3
Fisher *Martes pennanti*	11	23	41

Table 10. Cont.

Species	Stand Age, Years[a]		
	< 150	150-250	> 250
Long-tailed Weasel *Mustela frenata*	3	5	3
Short-tailed Weasel *Mustela ermina*		2	
Mink *Mustela vison*	3	6	
Spotted Skunk *Spilogale putorius*	29	32	31
Striped Skunk *Mephitis mephitis*	9	13	3
Bobcat *Lynx rufus*	15	3	5
Mule deer *Odocoileus hemionus*	86	85	85

[a]Sample sizes for age classes: < 150 = 35, 150-250 = 62, > 250 = 39

[b]Underlined percentages differed significantly among age classes ($p < 0.10$, chi-square).

[c]Single specimen found in small pond at edge of plot.

[d]Includes *Sorex trowbridgii* and *Sorex vagrans*.

[e]May include some records of *E. sonomae* (but we doubt it).

Table 11. List of species that are strongly associated with stand age, based on measures of frequency or abundance. Positive associations include species that are more abundant in older stands. Negative associations include those that are more abundant in younger stands.

Species	Evidence
Positive Association with old-growth	
Ensatina	Summer pitfalls
Pacific Shrew	Spring pitfalls
Other Sorex	Winter pitfalls
Coast Mole	Combined pitfalls
Deer Mouse	Winter pitfalls; livetrap 1981, 1982
Western Red-backed Vole	Winter, combined pitfalls
Allen's Chipmunk	Spring census, 1981-1982; track stations 1982; livetrap, 1982
Douglas's Squirrel	Track stations, 1981-1982, winter census 1981
Fisher	Cum. frequency
Dusky-footed Woodrat	Track stations, 1982
Chestnut-backed Chickadee	Spring census, 1981, 1982
Hermit Thrush	Spring census, 1981, 1982
Golden-crowned Kinglet	Spring census, 1981, 1982
Warbling Vireo	Spring census, 1981, 1982
Hermit Warbler	Spring census, 1981, 1982
Negative Association with old-growth	
Western Fence Lizard	Spring, summer, combined pitfalls, cum. frequency
Western Skink	Summer, combined pitfalls
Northern Alligator Lizard	Summer pitfalls; cum. frequency
Southern Alligator Lizard	Spring, combined pitfalls, cum. frequency
Western Gray Squirrel	Spring census, 1981; track stations, 1981; cum. frequency
Gray Fox	Track stations, 1981, 1982
Ringtail	Track stations, 1981; cum. freqency
Steller's Jay	Winter census, 1981, 1982

Table 11. Cont.

Species	Evidence
Brown Creeper	Spring census, 1981, 1982
American Robin	Spring census, 1981, 1982
Hermit Thrush	Winter census, 1981, 1982
Ruby-crowned Kinglet	Winter census, 1981, 1982
Solitary Vireo	Spring census, 1981, 1982
Nashville Warbler	Spring census, 1981, 1982
Black-throated Gray Warbler	Spring census, 1981, 1982
Western Tanager	Spring census, 1981, 1982
Black-headed Grosbeak	Spring census, 1981, 1982
Dark-eyed Junco	Spring census, 1981, 1982

[a]See Tables 3, 6, 7, 8 and 10 for data.

Our conclusions this year, based on 2 years of sampling, are much stronger than those of last year. When the next year of sampling is complete our conclusion will be even more sound.

To better understand relationships of wildlife species with old-growth forests, we should evaluate their habitat relationships along the full range of successional stages. An assessment of bird communities in early stages of Douglas-fir forest is now being conducted in northwestern California (Marcot and Meslow 1982). Mammal, reptile, and amphibian populations in these early stands are being evaluated by Raphael (1982). Conclusions regarding relations between species and stand age which are reported here may need modification when results of these other studies become available.

For example, Deer Mouse density was found to be positively correlated with stand age in our study. However, this species attained higher densities in clearcuts (Raphael 1982). Thus, one can not conclude that the Deer Mouse finds optimum habitat only in old-growth.

As a final note, we believe that the most important product resulting from our study will be a set of refined hypotheses about the dependency of wildlife on old-growth forests. Our conclusions are based strictly on correlations; such correlations do not necessarily reflect cause-and-effect relationships. We strongly advocate carefully controlled experiments and intensive, long-term behavioral studies as the next, necessary step to test the hypotheses we develop. We hope that this study will provide a solid foundation on which to build such experimental studies.

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